Does deterministic coexistence theory matter in a finite world? Insights from serpentine annual plants

Sebastian J. Schreiber[1,*], Jonathan M. Levine[2], Oscar Godoy[3], Nathan J.B. Kraft[4], and Simon P. Hart[2]

[1]Department of Evolution and Ecology and Center for Population Biology
University of California, Davis, USA 95616

[2]Institute of Integrative Biology
ETH Zürich (Swiss Federal Institute of Technology)
Universitätrasse 16, 8092 Zürich, Switzerland

[3]Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS-CSIC)
Av. Reina Mercedes 10
E-41080 Sevilla, Spain

[4]Department of Ecology and Evolutionary Biology
University of California, Los Angeles
Los Angeles, California, USA 90095

* Corresponding author: sschreiber@ucdavis.edu

Abstract: Much of the recent work on species coexistence is based on studying per-capita growth rates of species when rare (invasion growth rates) in deterministic models where populations have continuous densities and extinction only occurs as densities approach zero over an infinite time horizon. In nature, extinctions occur in finite time and rarity corresponds to small, discrete populations whose dynamics are not well approximated by deterministic models. To understand whether the biological significance of these discrepancies, we parameterized a stochastic counterpart of a classical deterministic model of competition using data from annual plants competing on serpentine soils. While the minimum of the invasion growth rates explained up to 60% of the variation in the predicted coexistence times, species pairs with similar invasion growth rates had coexistence times that differed by several orders of magnitude. By integrating the deterministic invasion growth rates and coexistence equilibrium population sizes, a simplified stochastic model explained over 99% of the variation in the coexistence times. This simplified model corresponds to uncoupled single species models whose parameters are determined from the two species model. This simplified model shows that coexistence times are approximately one-half of the harmonic mean of these single species' persistence times. Furthermore, coexistence times increase and saturate with invasion growth rates, but increase exponentially with equilibrium population sizes. When the minimum of the invasion growth rate is sufficiently greater than one, coexistence times of $1,000$ years occur even when the inferior species has < 50 individuals at the deterministic coexistence equilibrium. When the fitness inferior has the lower equilibrium population size (which occurs for 6 out of 8 of the deterministically coexisting pairs), niche overlap and fitness differences negatively impact coexistence times, which is consistent with the deterministic theory. However, when the fitness inferior has the higher equilibrium population size (2 species pairs), coexistence times can exhibit a humped shaped relationship with fitness differences–increasing and then decreasing with fitness differences. Collectively our results support the use of deterministic theory to infer the controls over coexistence in finite systems, while also highlighting when ecologists must look beyond invasion growth rates and consider species equilibrium population sizes.

Introduction

Observations of species rich ecological communities have motivated generations of ecologists to explore how species in nature coexist despite competitive imbalances. Although these species are inevitably characterized by finite populations, and can therefore only coexist for finite time periods, finiteness is ignored by the vast majority of approaches for understanding coexistence. This includes theory based on the study of deterministic equations assuming continuous variation in population density, and the increasing number of empirical studies that parameterize theoretical models to infer the controls over coexistence. Much of ecology is therefore implicitly assuming that the factors contributing to coexistence in mathematical frameworks conditioned on infinitely large population size similarly affect coexistence times in finite systems, or that population sizes are so large that finiteness can be safely ignored. Nonetheless, how much ecologists are missing by working from theory and tools assuming infinitely large populations or continuous variation in density when studying the coexistence of finite populations in nature is simply unknown.

Perhaps the most obvious place coexistence theory depends on continuous variation in population density is its use of the mutual invasibility criterion for pairs of competing species [Chesson and Ellner, 1989, Roth et al., 2017]. This criterion is met when each species can recover after its

population is depressed to vanishingly low density. In the simplest case, if species' invasion growth rates are positive then their populations reach a fixed point, oscillatory, or stationary distribution at which they persist for infinite time. Moreover, much recent progress in both our empirical and theoretical understanding of species coexistence has come from decomposing the invasion growth rate into quantities relevant to leading hypotheses about species diversity maintenance- the stabilizing niche difference and the average fitness difference [Chesson, 2000]. While these and other coexistence concepts described thus far relate to the mutual invasibility criterion, similar assumptions of continuously varying population density underlie linear stability analysis, another common theoretical approach for understanding species coexistence [May, 1975].

Despite the power of concepts derived under the assumption of continuous variation in population density to organize our thinking on species coexistence, their relevance to a natural world in which populations are composed of discrete individuals is far from clear [Jagers, 2010, Schreiber, 2017]. In contrast to the indefinite coexistence possible for populations with continuously varying density, coexistence in populations composed of discrete individuals is only possible over a finite period of time because such populations inevitably drift to extinction [Schreiber, 2017]. How well metrics predicting long term stable coexistence based on deterministic theory predict coexistence times in the finite systems of nature–the true object of study–remains unexplored. For example, while we rely on positive invasion growth rates to infer long term coexistence, finite populations with positive deterministic growth rates when depressed to very low numbers may still have a high extinction risk due to the effects of demographic stochasticity. More generally, the population ecology literature shows that the expected time to extinction of a population depends critically not only on the intrinsic rate of growth, but also on the equilibrium population size i.e the equilibrium population density times habitat size [Boyce, 1992, Grimm and Wissel, 2004, Ovaskainen and Meerson, 2010]. Similarly, we expect a strong influence of habitat size and equilibrium densities on coexistence times. Nonetheless, given that habitat size plays no role in determining the coexistence of populations with continuously varying densities, it is generally ignored in modern developments of coexistence theory, and in empirical tests of that theory. Finally, if the invasion criterion is suspect for finite populations, then so too might be the concepts derived from it, including stabilizing niche differences and average fitness differences. In sum, an analytical coexistence theory based on invasion growth rates and long term persistence cannot directly apply to competitive systems with finite populations. The question then becomes how useful are these concepts in a finite world, and which other variables are required to predict coexistence times?

Quantitatively addressing the controls over species diversity maintenance in finite systems is challenging due to the absence of analytical expressions for coexistence times as well as the absence of empirical data needed to ground theoretical results. Inconveniently, the most prominent body of ecological theory on species coexistence built on finite populations- the neutral theory- ignores the forces stabilizing coexistence and those driving competitive exclusion, and is therefore not helpful in resolving these issues. One path forward, and the one we develop here builds on the findings of Faure and Schreiber [2014]. These authors derive explicit relationships between the quasi-stationary behavior of stochastic models and their deterministic counterparts, with the goal of estimating intrinsic coexistence times in finite systems–the mean time where all species persist when the community dynamics are quasi-stationary [Grimm and Wissel, 2004]. These advances in conjunction with probabilistic algorithms for estimating these intrinsic coexistence times [Aldous et al., 1988, Benaïm and Cloez, 2015] allow us to explore the relationship between coexistence times for finite competing populations and the deterministic theory of coexistence.

Even accounting for the quantitative advances possible with techniques developed by Faure and Schreiber [2014], theoretical insights into the controls over coexistence times in finite systems will inevitably hinge on the demographic rates and competitive parameters of the interacting species. Yet this information, along with the total population size of the competitors, are rarely available for field systems of competitors. We overcome this hurdle here by working with a unique dataset of demographic rates and competitive interaction coefficients for annual plant species living on serpentine soils in California [Gilbert and Levine, 2013, Godoy et al., 2014]. These data allow us to bound our theoretical study of the controls over coexistence times with field-observed competitive rates.

In this paper, we explore how the necessarily transient coexistence found in finite systems depends on the controls over diversity maintenance developed for systems with continuously varying population density, as well as other factors not considered in contemporary coexistence theory such as population size. We first explore how the invasion growth rate and equilibrium population size for pairs of species in our serpentine annual community relate to their predicted coexistence times. We then use a simplified model to show that just these two factors- the invasion growth rate and equilibrium population size from a deterministic, mean field model- are sufficient to very accurately predict the coexistence times of the different competitor pairs in a finite system. With this simplified model, we explore how niche overlap and fitness differences, which simultaneously influence invasion growth rates and equilibrium population sizes, determine how long species coexist. We identify cases where the invasion growth rates do not match up with species equilibrium population sizes, generating counterintuitive relationships between fitness differences and coexistence times. More generally, our results suggest that the effects of finite population sizes on coexistence are relatively small, justifying the use of metrics of coexistence based on continuously varying populations in most biologically reasonably scenarios.

Models and Methods

The Model. We explore coexistence times in a system with two annual plant species with population sizes N_1 and N_2 living in a habitat of size S i.e. the total area or volume inhabited by the competing populations. Hence, the density of species i equals $n_i = N_i/S$. In the absence of competition, individuals of species i produce a Poisson number of offspring with mean λ_i i.e. the intrinsic fitness of species i. We assume that $\lambda_i > 1$ for both species. Intra- and inter-specific competition reduce the expected number of offspring of species i in the following density-dependent manner

$$\frac{\lambda_i}{1 + (\alpha_{ii} n_i + \alpha_{ij} n_j)(\lambda_i - 1)} \tag{1}$$

where α_{ii} and α_{ij} are intra- and inter-specific competition coefficients, respectively. The multiplicative factor of $\lambda_i - 1$ means that the interaction coefficients are in units of proportional reductions in λ such that when $\alpha_{ii} n_i + \alpha_{ij} n_j = 1$ the population is no longer expected to grow. As discussed below, the conditions for coexistence and exclusion for the deterministic, mean field model then correspond to the classical conditions for coexistence for the continuous-time Lotka-Volterra competition models.

Let $N_{i,t}$ and $n_{i,t} = N_{i,t}/S$ denote the population size and density, respectively, of species i in year t. In a finite system, if each individual within a species produces a Poisson number of offspring

with mean (1), then the update rule for our individual-based model is

$$N_{i,t+1} = \text{Poiss}\left(\frac{\lambda_{\text{i}} \text{N}_{\text{i,t}}}{1 + \sum_{\text{j}=1}^{2} \alpha_{\text{ij}} \text{n}_{\text{j,t}} (\lambda_{\text{i}} - 1)}\right) \quad \text{i, j} = 1, 2 \text{ and j} \neq \text{i} \tag{2}$$

where Poiss(μ) denotes a Poisson random variable with mean μ.

When the habitat size S is sufficiently large, the dynamics of $n_{i,t}$ of our individual-based model (2) are well-approximated by the deterministic, mean field model

$$\bar{n}_{i,t+1} = \frac{\lambda_i \bar{n}_{i,t}}{1 + \sum_{j=1}^{2} \alpha_{ij} \bar{n}_{j,t} (\lambda_i - 1)}. \tag{3}$$

Specifically, for any prescribed time interval, say $[0, T]$, $n_{i,t}$ is highly likely to remain arbitrarily close to $\bar{n}_{i,t}$ provided that S is sufficiently large and $n_{i,0} = \bar{n}_{i,0}$ (Appendix S1). Intuitively, for fixed initial densities of both species, larger habitat sizes correspond to greater population sizes and, consequently, smaller stochastic fluctuations in their densities. However, after enough time, both species eventually go extinct in finite time for the individual-based model unlike the deterministic, mean field model (Appendix S1).

The deterministic model (2), in a different parametric form, was developed by Leslie and Gower [1958] and had its dynamics fully characterized by Cushing et al. [2004]. We describe this characterization using our parameterization. As with the classical Lotka-Volterra competition model, competitive outcomes for the mean-field model are determined by two quantities: the niche overlap (ρ) and the average fitness difference $\frac{\kappa_j}{\kappa_i}$ of the two species [Chesson, 2013] where

$$\rho = \sqrt{\frac{\alpha_{12}}{\alpha_{22}} \frac{\alpha_{21}}{\alpha_{11}}} \text{ and } \frac{\kappa_j}{\kappa_i} = \sqrt{\frac{\alpha_{ii} \alpha_{ij}}{\alpha_{jj} \alpha_{ji}}}. \tag{4}$$

The niche overlap term describes the degree to which interspecific interactions approach intraspecific interactions, and determines the degree to which species gain demographic advantages when they drop to low relative population size. Low niche overlap means greater growth rates when rare and more stabilized coexistence. By contrast, the fitness difference drives competitive exclusion, favoring the growth of the fitness superior over the inferior. When $\frac{\kappa_j}{\kappa_i}$ is greater than one, species j is less impacted by competition and, therefore, species j displaces species i when there is complete niche overlap. In the deterministic, mean field model, the niche overlap and fitness difference determine whether two species will coexist via their contributions to species growth rate when rare, termed the invasion growth rate.

To set the baseline for examining the effects of niche overlap and the fitness difference on coexistence times in finite systems, we next describe how these quantities determine infinitely long-term coexistence in the deterministic, mean field model. To calculate the invasion growth rate of species i under the assumptions of the deterministic, mean field model, we first require the single species carrying capacity of the resident species j, which for this model is $\frac{1}{\alpha_{jj}}$. Inserting this value into equation (1) and assuming that species i is so rare as to have negligible effect on its own growth rate gives the invasion growth rate of species i:

$$\mathcal{I}_i = \frac{\lambda_i}{1 + (\alpha_{ij}/\alpha_{jj})(\lambda_i - 1)}. \tag{5}$$

This invasion growth rate can then be expressed in terms of the niche and fitness differences between the competitors by substituting in the niche overlap and fitness difference expressions from equation (5):

$$\mathcal{I}_i = \frac{\lambda_i}{1 + \rho(\kappa_j/\kappa_i)(\lambda_j - 1)}. \tag{6}$$

The species coexist about a globally stable equilibrium if both have invasion growth rates greater than 1. This occurs if $\rho < \kappa_1/\kappa_2 < \frac{1}{\rho}$. In the event of coexistence for the deterministic, mean field model, equilibrium population sizes of the two species equal:

$$\bar{n}_i^* = \frac{1}{\alpha_{ii}} \frac{1 - \rho\kappa_j/\kappa_i}{1 - \rho^2}. \tag{7}$$

Quasi-stationary distributions and intrinsic coexistence times. To examine how invasion growth rates, niche overlap, and fitness differences affect coexistence times in finite systems, we require a method for calculating such times. Following Grimm and Wissel [2004], we use quasi-stationary distributions (QSDs) of the stochastic models to define an *intrinsic coexistence time*. When the competitors' population sizes fluctuate a long time before a species goes extinct, the quasi-stationary distribution characterizes the fraction of time spent in each community state (n_1, n_2) prior to the extinction of one or both species [Méléard and Villemonais, 2012]. When the community dynamics follow the QSD, the probability p of losing a species is constant through time. Hence, the distribution of extinction times is geometric, and the mean time to losing the first species–equivalent to the mean time for which both species coexist–is $1/p$. We call $1/p$, the *intrinsic coexistence time* of the community. Appendix S2 provides precise definitions and describes simulation-based and analytical approaches to computing these QSDs and intrinsic coexistence times. The simulation-based approach [Aldous et al., 1988], which is presented here for the first time in the ecological literature, is computationally efficient as it only requires one simulation run of a suitably modified stochastic process whose rate of convergence to the QSD is exponential [Benaïm and Cloez, 2015].

Parameterization for Numerical Work. Quantifying the effect of invasion growth rates, niche overlap, and fitness differences on coexistence times in real-world communities requires knowledge of actual demographic rates and competitive strength from nature. To this end, we explored these effects in finite systems parameterized with values empirically derived from annual plant communities assembled on serpentine soils in California. In past work we have quantified the demographic rates and pairwise interaction coefficients between 18 species in a common field environment. In brief, we sowed focal individuals of each of these species into a density gradient of each of the competitors, allowing us to fit the per germinant seed production in the absence of neighbors and how fecundity declined with increasing neighbor density (including conspecific neighbors). The latter provided an estimate of the pairwise interaction coefficient following the functional form assumed in equation (1). We also measured the germination rate in the field plots and the survival of ungerminated seeds buried in nylon mesh bags. See Godoy et al. [2014] for full details on the methodology.

The full dynamics of the annual plant system can then be described by the following expression accounting for population growth from a seed bank and seeds produced from germinated individuals.

$$\bar{n}_{i,t+1} = \frac{r_i g_i \bar{n}_{i,t}}{1 + a_{ii} g_i \bar{n}_{i,t} + a_{ij} g_j \bar{n}_{j,t}} + (1 - g_i) s_i \bar{n}_{i,t} \qquad i \neq j, i = 1, 2, j = 1, 2 \tag{8}$$

where $\bar{n}_{i,t+1}$ is the density of seeds in the soil after seed production but prior to germination, g_i is the fraction of germinating seeds, s_i is seed survival, a_{ij} are competition coefficients for germinated individuals, and r_i are intrinsic yields of germinated seeds.

Assuming no seedbank (e.g. $g_i = 1$ or $s_i = 0$), this model is an alternative parameterization of equation (2). Given that including the seed bank greatly complicates our analysis, yet ignoring it would unfairly bias competition in the system, we chose to assume that seeds which ultimately germinate do so in the year after they are produced. If s_i is the probability of a seed surviving and g_i is its yearly germination probability, then the probability of ultimately germinating $\tilde{g}_i$ equals

$$\tilde{g}_i = g_i \left(1 + (1 - g_i)s_i + (1 - g_i)^2 s_i^2 + \dots\right) = \frac{g_i}{1 - (1 - g_i)s_i}.$$

The model in equation (9) then becomes:

$$\bar{n}_{i,t+1} = \frac{r_i \tilde{g}_i \bar{n}_{i,t}}{1 + a_{ii}\tilde{g}_i \bar{n}_{i,t} + a_{ij}\tilde{g}_j \bar{n}_{j,t}} \qquad i \neq j, i = 1, 2, j = 1, 2. \tag{9}$$

We parameterized the above expression with the empirical values for r_i, a_{ij}, s_i, and g_i. Note that this equation is equivalent to model (2) after setting $\lambda_i = r_i \tilde{g}_i$ and $\alpha_{ij} = \tilde{g}_j a_{ij}/(\lambda_i - 1)$. Therefore the coexistence times, invasion growth rates, niche overlap, and fitness differences can be calculated for the empirical system following the expressions outlined earlier in the methods.

Of all possible pairs of the 18 annual plant species, 8 were predicted to deterministically coexist. Using simulations of ten million years, we computed the intrinsic coexistence time for each of these 8 pairs with a range of habitat sizes (S). For subsequent analysis we set $S = 0.04$. This value of S would be empirically justified for the smallest hummocks in the landscape (those with a few m^2 of suitable habitat) for the subdominant species, which might contain as little as 20 individual plants, based on germinable densities projected from Gilbert and Levine [2013]. The species that compose the 8 focal pairs in our study tend to be more common and are often found on larger hummocks, but this small habitat size allows us to evaluate the dynamics of systems where the effects of finiteness can be explored. For 7 of the species pairs, multiple extinction events were recorded in the 10^7 years of the simulations. Consequently, for these 7 pairs we had good estimates for the intrinsic mean coexistence times C. For the final pair, there were no extinction events and we only have a lower bound of $> 10^7$ years for the intrinsic mean coexistence time. This outcome is consistent with the simplified model (see **Results**) providing an estimate of $C > 10^{15}$ for this species pair. Due to only having a lower bound for C, this species pair had to be excluded from some of our analyses.

Results

Can invasion growth rates and equilibrium population sizes predict coexistence times? We found a positive correlation between the minimal invasion growth rates and mean coexistence times across the seven focal pairs of competitors, as determined from the the quasi-stationary distributions of the empirically parameterized models (adjusted $R^2 = 0.6038$, $p = 0.0244$; Fig. 1A). More specifically, the lower of the two invasion growth rates predicts coexistence times. However, there was substantial variation in coexistence times unexplained by invasion growth rates, such that similar invasion growth rates resulted in several orders of magnitude difference in coexistence times.

We similarly found a positive correlation between the equilibrium population size of the less abundant species and coexistence times (adjusted $R^2 = 0.3386$; $p = 0.09964$, Fig. 1B). As the equilibrium population sizes did a worse job of explaining the variation in the coexistence times than the invasion growth rates, similar equilibrium population sizes also resulted in several orders of magnitude of difference in coexistence times.

We further found that the effect of invasion growth rates and populations size interact to determine coexistence times (Fig. 2). For all coexisting pairs, the larger the habitat size S, which scales population size, the longer the predicted coexistence time. More specifically, as predicted by [Faure and Schreiber, 2014], these coexistence time increase exponentially with habitat size (Fig. 2A, Appendix S3). Importantly, this relationship depended on the minimal invasion growth rate (see $\min_i \mathcal{I}_i$ in Fig. 2B associated with lines in Fig. 2A). Specifically, for five of the pairs, where even the lower of the two invasion growth rates was still well above 1, coexistence times increased rapidly with very small increases in habitat size. Yet for two others, where the lower invasion growth rate was much closer to 1, coexistence time increased more slowly with habitat size. This implies that to obtain any given coexistence time, pairs with lower minimal invasion growth rates require larger habitat sizes. Indeed, to obtain $1,000$ years of coexistence, for example, pairs with high invasion growth rates (> 2) require minimal equilibrium populations sizes $S \times \min\{\bar{n}_1^*, \bar{n}_2^*\}$ of approximately only 10 individuals, while the species pair with the lowest invasion growth rate (< 1.01) requires over 200 individuals for the minimal equilibrium population sizes (Fig. 2B). This implies that for systems where invasion growth rate are well above 1, finiteness and the equilibrium population sizes $S\bar{n}_i^*$ will play little role in predictions of coexistence.

To evaluate how well coexistence times could be quantitatively predicted by the combined effects of just equilibrium population sizes and invasion growth rates, we developed a simplified model. This model predicts coexistence times from two uncoupled stochastic single species models. Though uncoupled, each species in this model has a low density growth rate "λ_i" and carrying capacity "$1/\alpha_{ii}$" that matches its invasion growth rate $\mathcal{I}_i$ and equilibrium density $S\bar{n}_i^*$, respectively, from the deterministic two species model. Knowing the persistence times P_i of each of the species, we can calculate the coexistence time $C_{\text{simplified}}$ with the following expression (Appendix S4):

$$C_{\text{simplified}} = \frac{P_1 P_2}{P_1 + P_2 - 1}. \tag{10}$$

As long as the intrinsic persistence times P_i for each species are long enough (e.g. 10 years or more), the coexistence time predicted by the simplified model is approximately one half of the harmonic mean of the intrinsic persistence times for the two species: $C_{\text{simple}} \approx \frac{1}{2} \times \frac{1}{\frac{1}{2}\frac{1}{P_1} + \frac{1}{2}\frac{1}{P_2}}$. This expression makes clear that the species with the shorter persistence time contributes disproportionately to reductions in the coexistence time. In sum, the simplified model effectively allows competition to affect invasion growth rates and equilibrium population sizes. Nonetheless, the stochastic dynamics of the two competitors are completely uncoupled, allowing one to calculate the coexistence time from the single species persistence times.

For the 7 species pairs predicted to coexist in the deterministic model, the simplified model incorporating just invasion growth rates and equilibrium population sizes did an exceptional job in predicting the actual coexistence time ($\log C = 1.031 \log C_{\text{simple}}$ with $R^2 = 0.9977$ and $p < 10^{-8}$, Fig. 3). Even when the empirical parameters for these pairs were perturbed to explore a wider range of parameter values, similar results were obtained.

The relationship between competitor persistence time and invasion growth rates and equilibrium population sizes. Given that we have shown that multispecies coexistence times are well predicted from the persistence times of the individual competitors, we can gain insight into coexistence times by understanding the determinants of single species persistence times, a much simpler problem. In fact, in the limit where one of the species persists for very long time scales, the persistence time of the other competitor is the coexistence time ($\lim_{P_i \to \infty} P_1 P_2/(P_1 + P_2 - 1) = P_j$ in equation (10)).

The intrinsic persistence time P_i of species i in the simplified model increases with both the invasion growth rate $\mathcal{I}_i$ and the equilibrium population size $S\bar{n}_i^*$ (Appendix S3). However, it does not increase with these drivers of persistence in the same way. The intrinsic persistence time increases exponentially (i.e. linear in a log scale) with the equilibrium population size (Fig. 4A), yet in a saturated manner with the invasion growth rate (Fig. 4B). The reason the invasion growth rate has saturating effects on persistence times relates to the fact that high invasion growth rates can at best result in an expected population size next year equaling the equilibrium population size (whenever at least one individual is present in the current year). Hence, in this limit, extinction is set by the probability that all individuals with a Poisson distribution with mean $S\bar{n}_i^*$ go extinct. The chance of this catastrophic event occurring is $\exp(-S\bar{n}_i^*)$. Therefore, the limiting intrinsic persistence time for species i (dashed line in Fig. 4B) is

$$P_i \approx \exp(S\bar{n}_i^*) \text{ for } \mathcal{I}_i \text{ sufficiently large.} \tag{11}$$

We next look at the combined effects of the two determinants of persistence time (Fig. 4C) over an empirically relevant range of values. With a high invasion growth rate (e.g. above 4), population persistence time can only be increased by increasing the equilibrium population size. Similarly with a high equilibrium population size (e.g. above 40), persistence times can only be (markedly) increased by increasing the invasion growth rate. Only at lower values of these two determinants of persistence time (where the contours are curved), can the persistence time be increased both by changes in invasion growth rate or equilibrium population size (Fig. 4C).

Finally, with the white line in Fig. 4C, we show the combination of invasion growth rates and equilibrium population sizes that yield an expected persistence time of $1,000$ years, a time scale beyond the scope of nearly all ecological studies. For populations with invasion growth rates of 2 or more and equilibrium population sizes of approximately 10 individuals, persistence times are expected to be $1,000$ years. Courtesy of equation (10), these persistence times are on the same scale as expected coexistence times. Indeed, the shape of the relationship between the invasion growth rate and equilibrium population size required for $1,000$ years of persistence based on the simplified model mirrors that shown for the actual coexistence times in Fig. 2B.

How do niche overlap and fitness differences impact coexistence times? According to deterministic coexistence theory, niche overlap and fitness differences both have a detrimental impact on coexistence [Chesson, 2000, Adler et al., 2007]. As confirmed for our model (Appendix S5), this conclusion stems from niche overlap and fitness differences always reducing the invasion growth rates and equilibrium population sizes of the competitively inferior species (panels A–B and D–E in Figs. 5,6). Thus, with greater niche overlap ρ or larger fitness ratios κ_j/κ_i, the fitness inferior recovers more slowly when perturbed to low densities and tends to recover to a lower equilibrium density. To explore how these effects translate to coexistence times for finite populations, we varied

the niche overlap and fitness ratio for the 7 coexisting species pairs with $C < 10^7$ years. We wish to assess the effects of niche overlap independent of any change in fitness differences and vice versa. To do this we varied niche overlap between a pair of competitors, while holding the fitness difference constant, by multiplying the interspecific interaction coefficients α_{12}, α_{21} by a fixed factor. Separately (but similarly), we varied the fitness difference between a given pair of competitors, while holding the niche overlap constant, by multiplying α_{22}, α_{21} by a fixed factor.

As highlighted in equation (11), coexistence times for the simplified model depend disproportionately on the species with shorter persistence time. For all 7 pairs of coexisting species, the persistence time P_i of one species was at least 90 times greater than the persistence time of the other species. Consequently, the persistence of the more vulnerable species is strongly correlated with the community coexistence time (Spearman's rank correlation coefficient of 0.9642857). For the majority of the species pairs (5 out of 7), as would be expected, the fitness inferior was the competitor with the greater risk of extinction due to a lower invasion growth rate and a lower equilibrium population size. In these cases, numerical explorations of the full model support the predictions from the deterministic theory: increasing the niche overlap or fitness ratio of the fitness superior reduces coexistence times (Fig. 5C,F).

For two species pairs, however, the fitness superior was at greater risk of extinction because it has a lower equilibrium population size than the fitness inferior. In such cases, the effects of the fitness difference and niche overlap on coexistence times can become complex. This complexity stems from the fact that as the niche overlap or the fitness advantage of the fitness superior increases, so too can its invasion growth rate and equilibrium population size, potentially lengthening coexistence times. If the niche overlap or fitness difference get large enough, the fitness inferior will once again be the species with the lower invasion growth rate and equilibrium population size (Fig. 6B,E). Thus, the minimum of the equilibrium population sizes can exhibit a humped shaped relationship with increasing niche overlap or fitness differences (as seen in the shaded lines of Fig. 6B,E). By contrast, the minimum invasion growth rate for this focal species pair always decreased with the increasing niche overlap and fitness difference (Fig. 6A,D). Due to the relative strength of these countervailing effects, coexistence times decrease with increasing niche differences (due to a stronger invasion growth rate effect), and exhibit a humped-shaped relationship with increasing fitness differences (Fig. 6C,F). A similar humped shaped relationships were observed for two of the other species pairs (species pairs #2,8 in Appendix S6) when decreasing, rather than increasing, fitness differences. For one of these pairs (pair #2) the fitness superior had a lower equilibrium population size only at lower fitness differences than the empirically estimated fitness difference. However, for neither of these pairs, did eliminating fitness differences (i.e. setting κ_j/κ_i to one) result in a greater coexistence time.

Finally, we examined the joint effect of niche overlap and fitness differences on coexistence times (Fig. 7). As predicted from the univariate relationships, when the fitness inferior is more susceptible to extinction, coexistence time decreased with increasing niche overlap and fitness differences (Fig. 7A). In contrast, when the fitness superior is more susceptible to extinction, coexistence times exhibited more complex relationships with fitness differences (Fig. 7B).

Discussion

Deterministic coexistence theory has proven powerful and analytically convenient [Chesson, 2000, Adler et al., 2007, 2010, Ellner et al., 2016], but the extent to which its predictions diverge from reality when describing the maintenance of species diversity in finite systems has largely been ignored. While recent developments in deterministic theory focus on invasion growth rates as the arbiter of coexistence, our results demonstrate that coexistence in finite populations can be limited either by invasion growth rates or equilibrium population sizes or both (Figs. 3 and 4). However, because niche overlap and fitness differences generally have predictable negative effects on both invasion growth rates and equilibrium population sizes, increasing both these quantities reduces coexistence times in most–but not all–cases (Figs. 5 and 6). More generally, we demonstrate that finite coexistence times based on deterministic coexistence predictions will often be exceedingly long for systems composed of more than ten to a few hundred individuals of the rarer species (Fig. 2), suggesting limited effects of finiteness in many empirically relevant scenarios.

For continuous density models of two competing species, mutual invasibility implies deterministic coexistence. Moreover, the higher the invasion growth rates, the more quickly species recover from being rare. Implicit in this approach to understanding coexistence is the expectation that species will coexist longer when all species in a community have higher invasion growth rates. Consistent with this expectation, we found that the minimum of the invasion growth rates for a species pair was positively correlated with their coexistence times. Alternatively, classical population viability theory predicts that equilibrium population sizes play a key role in species persistence: the greater the equilibrium population size of each species, the longer each species persists [Boyce, 1992, Mangel and Tier, 1994, Grimm and Wissel, 2004]. Consistent with this expectation, we found the minimum of the equilibrium population size of a species pair was correlated with coexistence times, but only with a significance level of $p = 0.09$. Despite these positive correlations, invasion growth rates and equilibrium population sizes, when considered separately, explained at most 60% of the variation in the coexistence times.

In contrast to the independent effects of invasion growth rates and equilibrium population sizes, our simplified model demonstrates that their combined effects describe over 99% of the variation in coexistence times. This simplified model evaluates the viability of each species independent of one another, but subject to the constraint that their equilibrium population sizes and low density growth rates are determined by their interaction with the other species. This simplification allowed us to more carefully dissect what drives the coexistence times for 8 pairs of deterministically coexisting species. In particular, for all pairs of deterministically coexisting species, one species is much more likely to go extinct before the other. As the coexistence time for the simplified model is approximately the harmonic mean of the persistence times of the competitively constrained individual species divided by the number of species, the species more likely to go extinct largely determines the coexistence time of the species pair.

Of the eight focal species pairs, the persistence time of the more vulnerable species was constrained mostly by its invasion growth rate in two of the cases, its equilibrium population size in two cases, simultaneously by both quantities in three cases, and neither in one case (Fig. 4C). Our analysis also revealed a fundamental difference in how equilibrium population sizes and invasion growth rates constrain persistence. Persistence times increase exponentially with equilibrium population size and, ultimately, large enough equilibrium population size can ensure persistence over arbitrarily large time frames despite lower invasion growth rates. This exponential increase in persistence times

is consistent with classical single species theory [Lande, 1993] and experimental work with *Daphnia magna* populations [Griffen and Drake, 2008]. In contrast, though persistence times increase with invasion growth rates, they saturate at a maximal value determined by the equilibrium population size. Our work illustrates how these classical population viability results operate in a multi-species context.

The maximal persistence time and ultimately the coexistence time can be surprisingly long for even small populations. For example, for two of the empirical pairs, the invasion growth rates for the more vulnerable species were sufficiently large (i.e. greater than 2) to ensure persistence times of approximately $1,000$ years with equilibrium population sizes of approximately 10 individuals of the rarer species. Of course, such persistence times are overly optimistic due to the models not accounting for Allee effects [Courchamp et al., 2008], sources of positive frequency-dependence such as reproductive interference [Gröning and Hochkirch, 2008, Weber and Strauss, 2016], or individual variation in demographic rates that increases extinction risk [Lloyd-Smith et al., 2005, Melbourne and Hastings, 2008, Hart et al., 2016]. Nonetheless, it does make the important point that when considering the controls over coexistence between species with strongly positive invasion growth rates, finiteness can justifiably be ignored.

In those cases where invasion growth rates are not so strongly positive, the influence of equilibrium population size can complicate the controls over coexistence from continuous density models. While in general, increasing niche overlap and fitness differences decreased coexistence times, as would be expected, in the less frequent case where the fitness superior was actually the less abundant species at equilibrium, more complex relationships could emerge. In particular, we found that for one of our empirical pairs, increasing fitness differences first increased and then decreased coexistence times due to effects on the equilibrium population size of the less abundant species. Given such a result depends on the fitness superior being the less abundant species at equilibrium, one can simply check whether this is the case, before interpreting the effects of niche overlap and fitness differences as they are commonly derived and applied [Chesson, 2000, Adler et al., 2007, 2010, Gilbert and Levine, 2013, Chesson, 2013]. According to equation (7), the fitness inferior has the larger equilibrium abundance when it is insensitive to intraspecific competition (i.e. has a large carrying capacity $1/\alpha_{ii}$) but highly sensitive to interspecific competition relative to the fitness superior. This observation provides an indirect means of evaluating whether this inverted relationship is likely to occur in a given empirical system.

Understanding how finiteness influences coexistence in higher dimensional communities with more than two species is a major challenge for future work. As we have done here, it may be possible to simplify our modeling of coexistence times in these higher dimensional communities by making an assumption common in coexistence theory for each species i in the community, there exists a unique $-i$ subcommunity [Chesson, 1994, Adler et al., 2010]. For example, if the entire community coexists at a stable equilibrium, and there is a unique stable equilibrium associated the removal of each competitor from the community (i.e. the $-i$ subcommunity equilibrium), then one can consider a simplified model where the dynamics of each species is characterized by its growth rate when invading its $-i$ subcommunity equilibrium and its population size at the full community equilibrium. If P_i is the persistence time of species i in this simplified model and there are no competitive intrasnsitivities (as typically is the case for the annuals considered here cf. Godoy et al. [2017]), then this model would predict a mean coexistence time of $C_{\text{simple}} = \frac{1}{1-\prod_{i=1}^{n}(1-1/P_i)}$. When the persistence times for each species are sufficiently large, then the coexistence time C_{simple}

is approximately the harmonic mean of the individual persistence times P_i. Hence, as in the two species case, the most vulnerable species has a disproportionately large effect on the community coexistence time.

Ultimately, ecologists would also benefit from understanding coexistence times when there are non-equilibrium dynamics, competitive intransitivities, and multiple $-i$ subcommunities. At this very general level, there is a mathematically rich theory where coexistence, in the sense of permanence, is determined by invasion growth rates [Schreiber, 2000, Garay and Hofbauer, 2003, Hofbauer and Schreiber, 2010, Roth et al., 2017]. Coexistence criteria in this theory involve finding a weighted combination of the species such that the resulting weighted average of the per-capita growth rates is positive whenever one or more species is rare. It seems likely that coexistence times should be positively correlated with these weighted averages.

In conclusion, we addressed the major motivating question of this paper: When should ecologists be wary of using continuous density coexistence metrics in finite systems? Our results suggests that in many if not most cases, the use of invasion growth rates, and niche overlap and fitness differences to understand coexistence in finite systems is theoretically justified. Certainly, if invasion growth rates are strongly positive (multiplicative annual growth rates of 2 or more), the influence of the equilibrium population size on coexistence in finite systems can be safely ignored. This is an important result for empiricists using invasion growth rates to project competitive outcomes. Moreover, even in cases where the invasion growth rate is closer to 1, the effects of increasing niche overlap and fitness differences on coexistence times in finite systems should match their qualitative effect in systems with continuous density, particularly when equilibrium population sizes are on the order of 50 to a few hundred individuals (Fig. 2B). The exception occurs in the less common case where the fitness superior is actually the less abundant species at equilibrium and therefore more susceptible to extinction. This was the case that generated a hump shaped relationship between fitness differences and coexistence times in our analysis (Fig. 6F), but this could be rare in nature as it only occurred for two of our eight empirical competitive pairs in our study. Other effects of finiteness can arise when individuals inherently vary in their vital rates and competitive traits, but past work shows that even this variation has modest effects on coexistence [Hart et al., 2016]. Only by developing the type of theory we have done so here can we justify the broad use of invasion growth rates, and its determinants- niche overlap and fitness differences- for predicting coexistence (times) in the inevitably finite systems found in nature.

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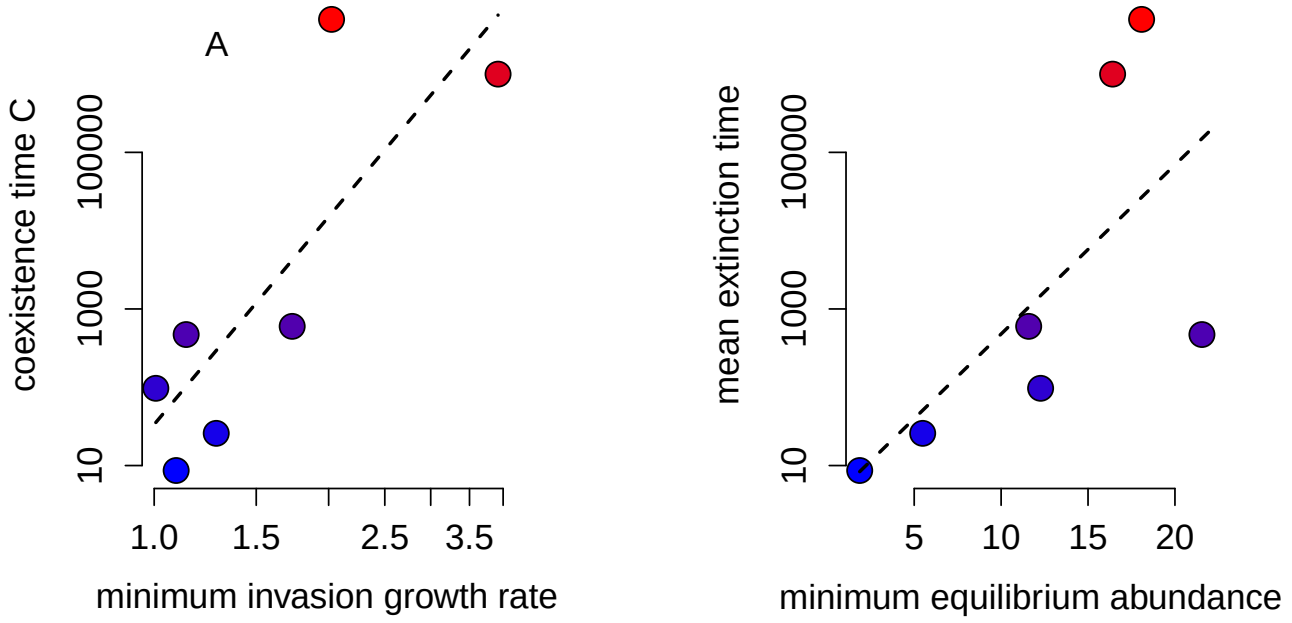


Figure 1: Predicting coexistence times using invasion growth rates (A) and equilibrium population sizes (B). Both panels plotted on a log–log scale.

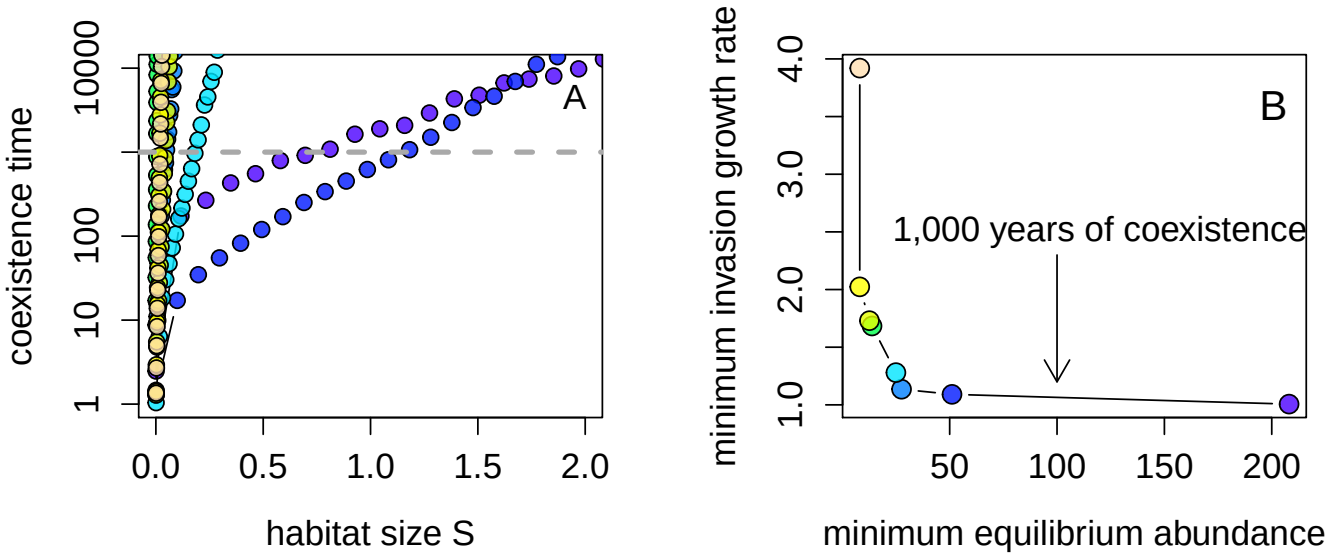


Figure 2: Coexistence times increase exponentially with habitat size S (A) for the 8 deterministically coexisting species pairs. $1,000$ expected years of coexistence (B) requires larger minimal equilibrium population sizes $S \times \min\{\bar{n}_1^*, \bar{n}_2^*\}$ for species pairs with lower minimal invasion growth rates. Colors for each species pair are the same in both panels.

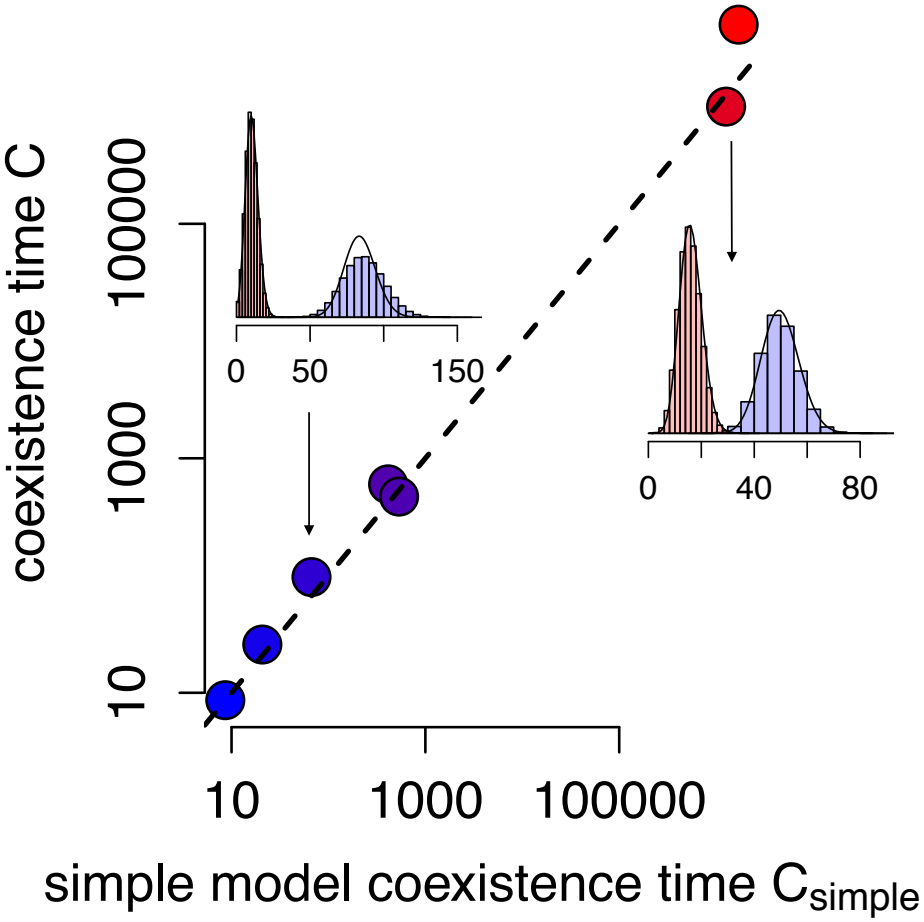


Figure 3: Predicting coexistence times with the simplified model. Dashed line is the 1-to-1 line. In the insets, quasi-stationary distributions of the coupled, competitive model and the simplified model. Bar plots are the simulation-based estimates of the competitive model's quasi-stationary distributions and black curves are the analytically based estimates from the simplified model.

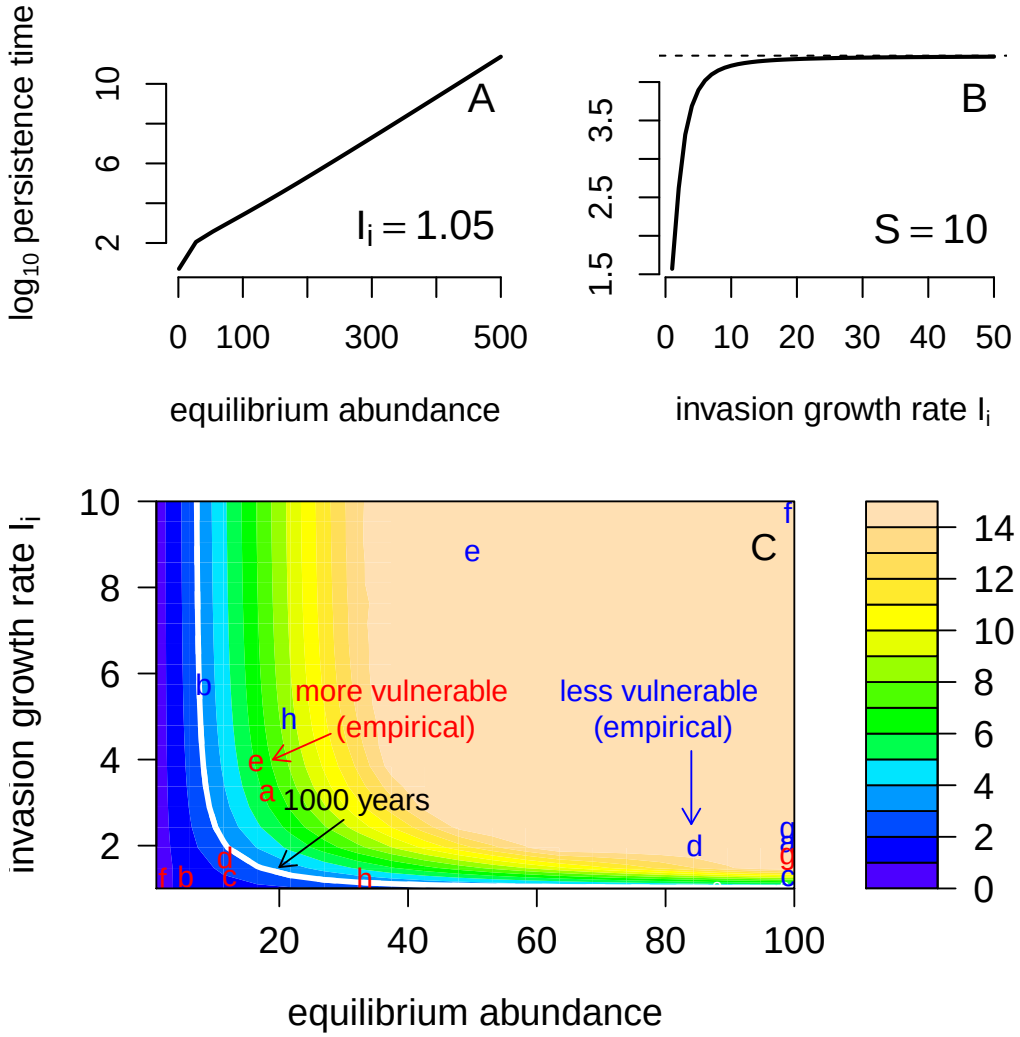


Figure 4: In A, asymptotically exponential growth of persistence times with equilibrium population population size. In B, persistence times increase and saturate with invasion growth rates. The dashed line corresponds to the analytic prediction $\exp(\hat{N}_i)$ in the large $\mathcal{I}_i$ limit. In C, $\log_{10}$ persistence times as a function of $\mathcal{I}_i$ and equilibrium population size. The white contour line corresponds to persistence times of $1,000$ years. Red/blue letters correspond to empirical values for species with the lower/higher persistence times for each of the coexisting species pairs.

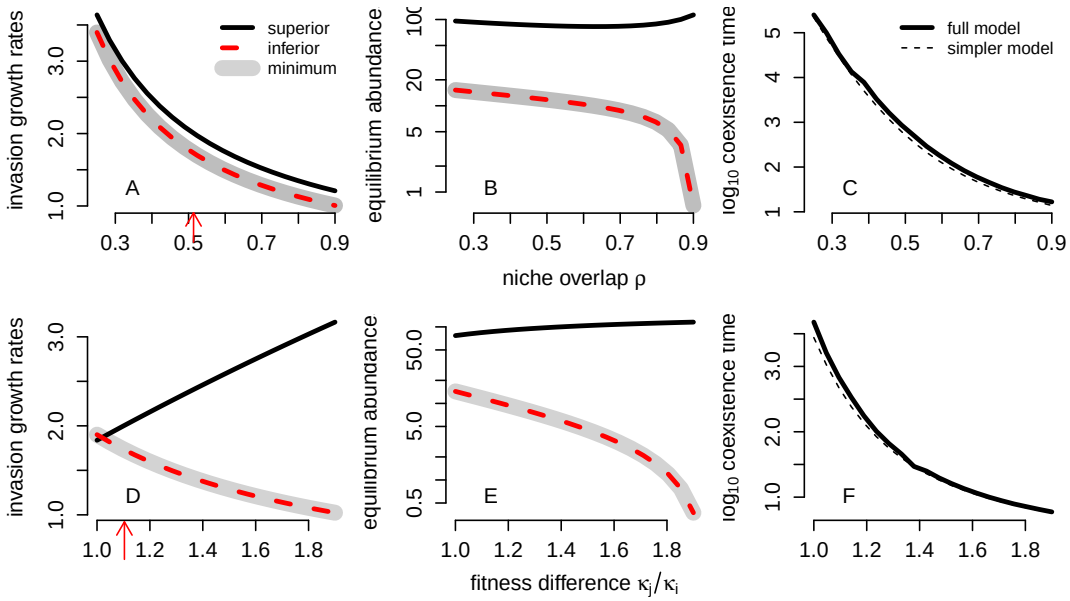


Figure 5: Effects of niche overlap and fitness ratios on coexistence times for a pair of competing species where the fitness inferior was at greater risk of extinction. In (A) and (D), the deterministic invasion growth rates of the deterministic, mean field model are plotted for the fitness inferior (dashed red) and fitness superior (solid black) with gray shading indicating the minimum of two invasion growth rates. In (B) and (E), the deterministic equilibrium population sizes $S\hat{n}_i$ are plotted with the gray shading indicating the minimum of the two population sizes. In (C) and (F), $\log_{10}$ coexistence times and the simpler model approximations (dashed lines) are plotted. Red arrows correspond to base empirical value.

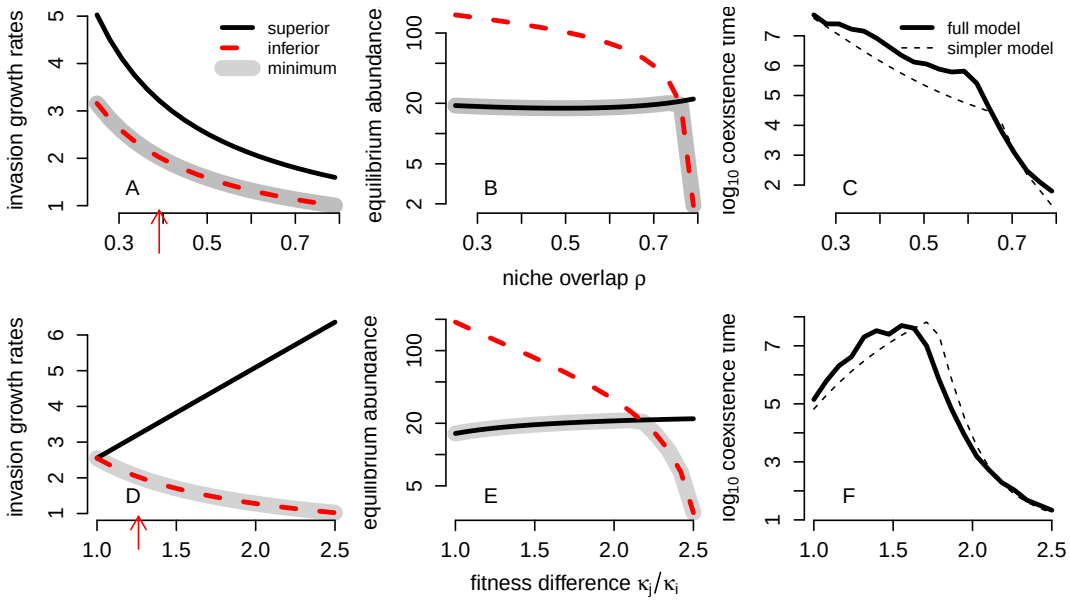


Figure 6: Effects of niche overlap and fitness ratios on coexistence times for a pair of competing species where the fitnes superior was at greater risk of extinction. In (A) and (D), the deterministic invasion growth rates of the deterministic, mean field model are plotted for the fitness inferior (dashed red) and fitness superior (solid black) with gray shading indicating the minimum of two invasion growth rates. In (B) and (E), the deterministic equilibrium population sizes $S\hat{n}_i$ are plotted with the gray shading indicating the minimum of the two population sizes. In (C) and (F), $\log_{10}$ coexistence times and the simpler model approximations (dashed lines) are plotted. Red arrows correspond to base empirical value.

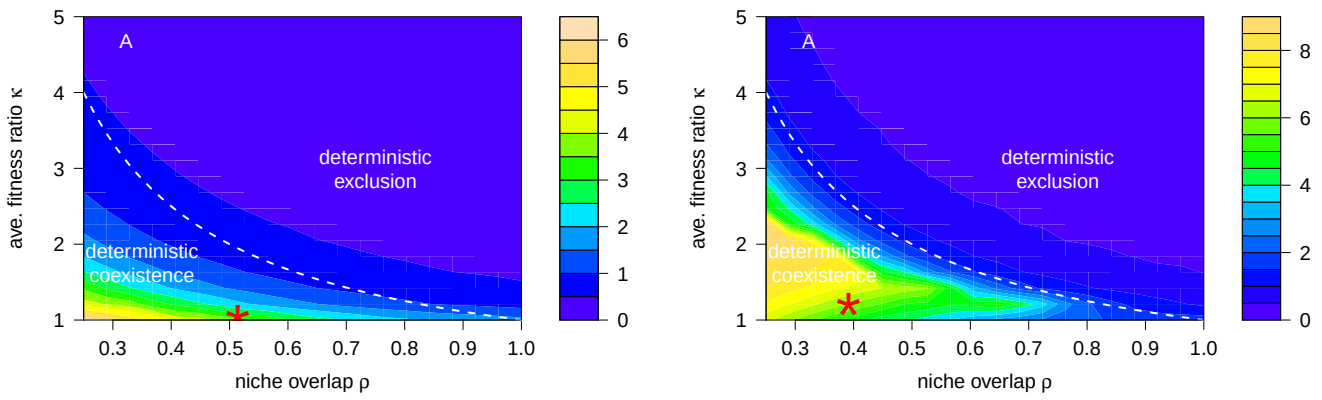


Figure 7: Joint effects of fitness ratios and niche overlap on coexistence times for two species pairs. The fitness inferior has the lower equilibrium population size in (a) and the higher equilibrium population size in (b). The plots show $\log_{10}$ coexistence times, which were calculated while varying fitness ratios and niche overlap around their empirical values (denoted by the red asterisks).

Appendix S1 Deterministic approximation and extinction

In this Appendix, we prove two results. First, we prove that for any given time frame $[0, T]$, the probability of stochastic model $n_t = (n_{1,t}, n_{2,t})$ deviating from the mean field model $\bar{n}_t = (\bar{n}_{1,t}, \bar{n}_{2,t})$ is arbitrarily small for $0 \leq t \leq T$ provided the habitat size S is sufficiently large. Second, we prove that, despite this strong correspondence over finite time frames, the stochastic models goes to extinction in finite time with probability one. To facilitate the presentation of these conclusions, define $f(n) = (f_1(n), f_2(n))$ where $f_i(n) = n_i\lambda_i/(1 + (\alpha_{ii}n_i + \alpha_{ij}n_j)(\lambda_i - 1))$ where $i, j \in \{1, 2\}$ and $i \neq j$. Let $M = \max\{\lambda_1/\alpha_{11}, \lambda_2/\alpha_{22}\}$. Notice that $f_i(n) \leq M$ for all $n = (n_1, n_2)$.

For the first assertion, let $T \geq 1$ and $\varepsilon > 0$ be given. Assume that $n_0 = \bar{n}_0$. We will show that

$$\lim_{S\to\infty} \mathbb{P}\left[\max_{0\leq t\leq T} \|n_t - \bar{n}_t\| \geq \varepsilon\right] = 0. \tag{12}$$

Continuity of f implies that there exists $\delta > 0$ such that $\max_{0\leq t\leq T} \|n_t - \bar{n}_t\| \leq \varepsilon$ whenever $\|f(n_{t-1}) - n_t\| \leq \delta$ for $1 \leq t \leq T$. As the mean and variance of a Poisson random variable are equal, Chebyshev's inequality implies

$$\mathbb{P}\left[\|f(n_{t-1}) - n_t\| \geq \delta\right] \leq \frac{M}{S\delta^2} \tag{13}$$

from which (12) follows.

For the second assertion, let

$$\beta = \min_{x\in[0,M]^2} \mathbb{P}[n_1 = 0 | n_0 = x] = \min_{x\in[0,M]^2} \exp\left(-S\sum_{i=1}^{2} f_i(x)\right) > 0.$$

Next we use the following standard result in Markov chain theory [Durrett, 1996, Theorem 2.3 in Chapter 5].

Proposition. Let X be a Markov chain and suppose that

$$\mathbb{P}\left[\bigcup_{s=1}^{\infty}\{X_{t+s} \in C\}\Big| X_t\right] \geq \beta > 0 \text{ on } \{X_t \in B\}.$$

Then

$$P\left[\{X_t \text{ enters } B \text{ infinitely often}\} \setminus \{X_t \text{ enters } C \text{ infinitely often}\}\right] = 0.$$

The proposition with $B = [0, M]^2$ and $C = \{(0, 0)\}$ implies that $\mathbb{P}[n_t = 0 \text{ for some } t \geq 1] = 1$.

Appendix S2 Quasi-stationary distributions and intrinsic coexistence times

In this Appendix, we give a precise definition of intrinsic coexistence times and describe the methods to compute them analytically and numerically. First, we define the quasi-stationary distribution precisely. Given a community in state $n = (n_1, n_2)$, define $n \gg 0$ to mean $n_1 > 0$ and $n_2 > 0$ i.e. both species are present in the community. Let $P(n, n')$ be the probability of going from state n to state n' in one time step i.e. P is the (infinite) transition matrix for the Markov chain n_t defined in the methods section. Let Q be the restriction of P to states where $n \gg 0$ and $n' \gg 0$ i.e. Q correspond to removing all the rows and columns corresponding to a state where one or both species are extinct. A quasi-stationary distribution [Méléard and Villemonais, 2012] for n_t is a probability distribution $q(n)$ (i.e. $\sum_n q(n) = 1$ and $q(n) \geq 0$) that corresponds to a left eigenvector of Q. Namely, there exists $0 \leq \eta < 1$ such that

$$Q(n') = \eta \sum_{n \gg 0} Q(n) P(n, n').$$

The quasi-stationary distribution corresponds to a distribution on the non-extinction states such that if the process n_t starts in the quasi-stationary distribution (i.e. $\mathbb{P}[n_0 = n] = q(n)$ for all $n \gg 0$), then extinction of one or both species occurs with probability $1 - \eta$ and on the event of non-extinction, the system remains in the quasi-stationary distribution. When the community is following the quasi-stationary distribution, the probability of losing one or both species is $1 - \eta$ in each time step. Hence, the coexistence time of the community (i.e. neither species goes extinct) is a geometric random variable with mean $1/(1 - \eta)$.

As our model (2) is an example of a nonlinear Poisson branching process (see, section 5.2 of Faure and Schreiber [2014] for a definition) whose mean-field dynamic (3) takes $[0, \infty)^2$ into the compact set $[0, \lambda_1/(\alpha_{11}(\lambda_1 - 1) \times [0, \lambda_2/(\alpha_{22}(\lambda_2 - 1))$ in one time step, Proposition 6.1 from Faure and Schreiber [2014] implies there is a unique quasi-stationary distribution of (2).

A key feature of unique quasi-stationary distributions is that they characterize the metastable behavior of the community dynamics conditioned on non-extinction. Namely, provided the limits exist (i.e. the Yaglom limit [Méléard and Villemonais, 2012]), one has

$$\lim_{t \to \infty} \mathbb{P}\left[n_t = n | n_t \gg 0\right] = q(n)$$

for any $n \gg 0$. That is, $q(n)$ describes the probability in the long-term that the community is in state n given that no species has gone extinct.

Numerical considerations. While it is possible to solve this eigenvalue-eigenvector problem for single species models (in fact we make use of this fact), solving this problem is computationally challenging for two species communities even with a small number of individuals. For example, even if each species in the community almost remains below 100 individuals (i.e. you can truncate the model to N_i remaining in the interval $[0, 100]$), the relevant truncated probability transition matrix is $100^2 = 10,000$ by $10,000$. Computing eigenvalues and eigenvectors for such large, non-sparse matrices is exceptionally difficult.

Fortunately, there is an alternative method which involves simulating a variant of the model

for sufficiently long periods of time. This alternative method developed by Aldous et al. [1988]. Specifically, whenever a species goes extinct, the modified process replaces this outcome by randomly assigning (with equal probability) a community state that was previously visited. The distribution of states visited in the long-run of this modified process converges to the QSD with probability one [Aldous et al., 1988]. Furthermore, the frequency of extinctions of each species for the modified process converges to their extinction probabilities in the quasi-stationary distribution. Hence, a single long run of the modified process provides all of the relevant information associated with metastable behavior of our model and the associated coexistence times.

Appendix S3 Quasi-stationary distributions and coexistence times for large habitat sizes

In this Appendix, we apply the results of Faure and Schreiber [2014] to the single species and competing species models presented in the text. First consider the two species model (2) when the deterministic model predicts coexistence i.e. $\mathcal{I}_i > 1$ for $i = 1, 2$. In this case, Cushing et al. [2004] proved that the coexistence equilibrium $(\bar{n}_1^*, \bar{n}_2^*)$ of the mean-field mdoel (3) is globally stable i.e. all initial conditions of the deterministic mean-field model supporting both species asymptotically approach this equilibrium. As the only invariant probability measure supported in $(0, \infty)^2$ for the mean-field model is the Dirac measure at this coexistence equilibrium, Lemmas 3.9 and Theorem 5.4 of Faure and Schreiber [2014] imply that (i) the quasi-stationary distributions converge in the weak* topology to this Dirac measure as $S \uparrow \infty$ and (ii) there exists a constant $C > 0$ such that the intrinsic coexistence time is $\geq \exp(CS)$ for sufficiently large habitat sizes S. Similar conclusion apply to the single species model as the mean-field model $\bar{n}_{t+1} = \bar{n}_t \frac{\lambda}{1+\alpha\bar{n}_t(\lambda-1)}$ has a globally stable equilibrium $\bar{n}^* = \frac{1}{\alpha}$ whenever $\lambda > 1$.

Appendix S4 Coexistence times for the Null Model

To determine the coexistence times for the null model, let P_i be the mean persistence time for each species. As these times are geometrically distributed, the probability of extinction in each time step is $1/P_i$ for species. As the two species dynamics are independent in the null model, the probability that neither goes extinct in a time step is $(1-1/P_1)(1-1/P_2)$, and the probability at least one goes extinct in a time step is $1-(1-1/P_1)(1-1/P_2)$. Hence, the mean time to losing one of the species is

$$\frac{1}{1-(1-1/P_1)(1-1/P_2)} = \frac{P_1P_2}{P_1P_2-(P_1-1)(P_2-1)} = \frac{P_1P_2}{P_1+P_2-1}$$

as claimed in the main text. For $P_1 \gg 1$ and $P_2 \gg 1$, we have

$$\frac{P_1P_2}{P_1+P_2-1} = \frac{1}{1/P_2+1/P_1-1/(P_1P_2)} \approx \frac{1}{1/P_1+1/P_2}$$

which equals $1/2$ of the harmonic mean of the $1/P_i$ as claimed in the main text.

Appendix S5 Analysis of equilibrium densities

This appendix analyzes how the equilibria densities of the deterministic model change with niche overlap ρ and the fitness difference κ_j/κ_i. Recall that at the coexistence equilibrium, the density of species i is given by

$$\bar{n}_i^* = \frac{1}{\alpha_{ii}} \frac{1-\rho\kappa_j/\kappa_i}{1-\rho^2}.$$

This expression is decreasing linearly with the fitness ratio κ_j/κ_i associated with species j i.e. as species j becomes a better competitor, the equilibrium density of species i decreases. The derivative of $\bar{n}_i^*$ with respect to ρ equals

$$\begin{aligned}\frac{\partial \bar{n}_i^*}{\partial \rho} &= \frac{1}{\alpha_{ii}} \frac{-(1-\rho^2)\kappa_j/\kappa_i + 2\rho(1-\rho\kappa_j/\kappa_i)}{(1-\rho^2)^2} \\ &= \frac{\kappa_j}{\alpha_{ii}\kappa_i} \frac{-\rho^2 + 2\rho\kappa_i/\kappa_j - 1}{(1-\rho^2)^2}\end{aligned}$$

When $\kappa_i/\kappa_j < 1$ (i.e. species i is the fitness inferior), the numerator is negative for all $\rho \geq 0$. Hence, the equilibrium density of the fitness inferior decreases with niche overlap, as claimed in the main text. In contrast, when $\kappa_i/\kappa_j > 1$ (i.e. species i is the fitness superior), the numerator of this derivative is negative for $\rho < \rho_i/\rho_j - \sqrt{\rho_i^2/\rho_j^2 - 1}$ and positive for $\rho > \rho_i/\rho_i - \sqrt{\rho_i^2/\rho_j^2 - 1}$. In particular, as coexistence only occurs, in this case, for $\rho < \kappa_j/\kappa_i$ and

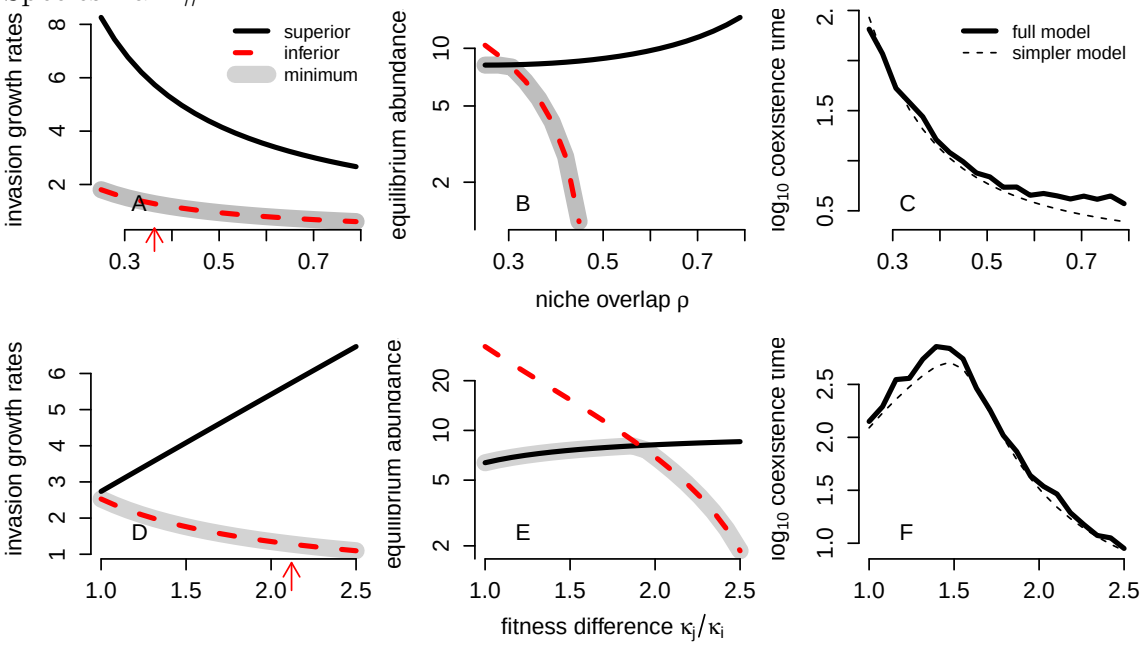
$$\frac{\partial \bar{n}_i^*}{\partial \rho}\Big|_{\rho=\kappa_j/\kappa_i} = \frac{\kappa_j}{\alpha_{ii}\kappa_i} \frac{-(\kappa_j/\kappa_i)^2 + 1}{(1-\rho^2)^2} > 0 \text{ as } \kappa_j/\kappa_i < 1$$

the equilibrium density of the fitness superior decreases and then increase with niche overlap.

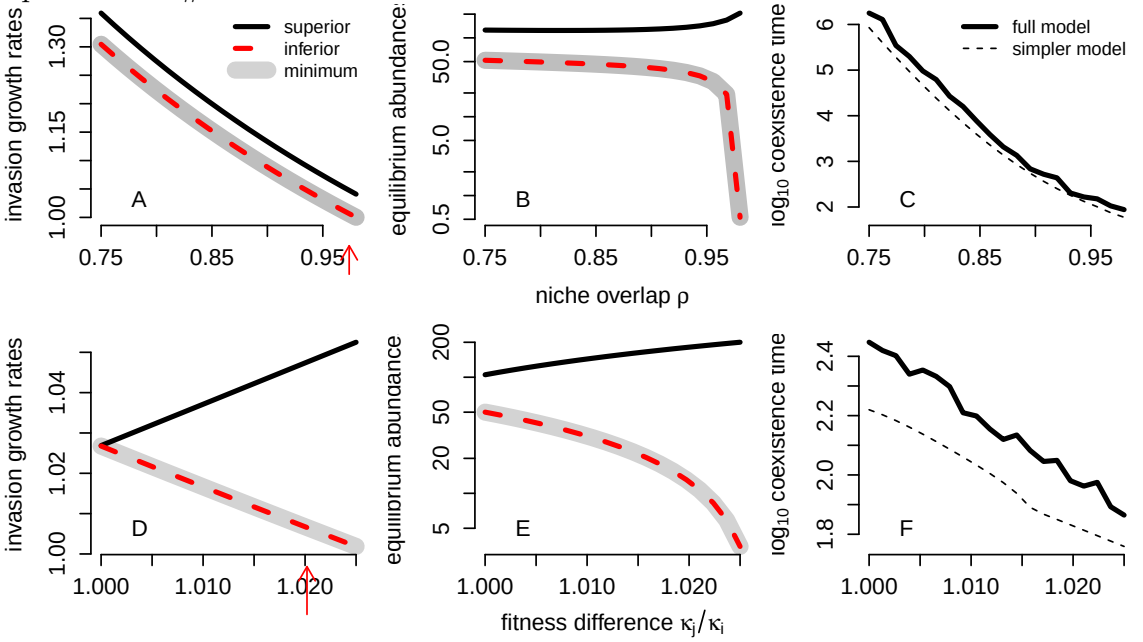
Appendix S6 Effects of ρ and κ_j/κ_i on coexistence times

In this Appendix, we explored the effects of ρ and κ_i/κ_j of the fitness superior for 5 of deterministically coexisting pairs; the results for the other two species pairs (#1,#4) are shown in Figs. 5,6 in the main text. Red arrows correspond to base empirical value.

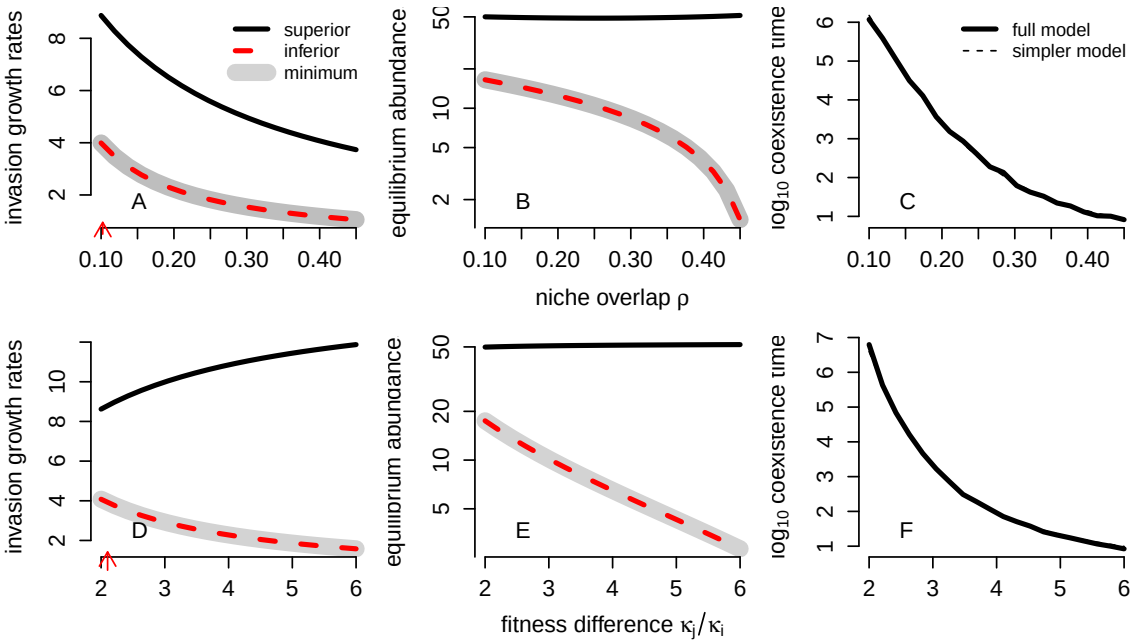
Species Pair #2



Species Pair #3



Species Pair #5



Species Pair #6